



**HAL**  
open science

# Limiting Feller diffusions for logistic populations with age-structure

Sylvie Méléard, J.A.J. Metz, Viet Chi Tran

► **To cite this version:**

Sylvie Méléard, J.A.J. Metz, Viet Chi Tran. Limiting Feller diffusions for logistic populations with age-structure. 2011. hal-00595928v1

**HAL Id: hal-00595928**

**<https://hal.science/hal-00595928v1>**

Preprint submitted on 26 May 2011 (v1), last revised 18 Aug 2011 (v2)

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Limiting Feller diffusions for logistic populations with age-structure

Méléard, Sylvie

*Ecole Polytechnique, Centre de Mathématiques Appliquées, UMR CNRS 7641,*

*Route de Saclay, 91128 Palaiseau Cedex, France.*

*E-mail: sylvie.meleard@polytechnique.edu*

Metz, J.A.J

*Mathematical Institute & Institute of Biology & NCB Naturalis, Leiden,*

*Niels Bohrweg 1, 2333 CA, Leiden, Netherlands.*

*& EEP, IIASA, Laxenburg, Austria.*

*E-mail: j.a.j.metz@biology.leidenuniv.nl*

Tran, Viet Chi

*Université des Sciences et Technologies Lille 1, Laboratoire Paul Painlevé, UMR CNRS 8524,*

*Cité Scientifique, 59655 Villeneuve d'Ascq Cedex, France.*

*E-mail: chi.tran@math.univ-lille1.fr*

Population dynamics with age structure are very important in demography and ecology since the demographic parameters of most species change over their life (think of maturation and senescence) and many phenomena (*e.g.* evolving life histories or kinship based social interactions such as cooperative breeding) require the introduction of age for their proper description (*e.g.* [4]). Evolution in general structured population is treated on a physical level of rigor in Durinx *et al.* [6] and Metz [20]. We consider here a long time scale diffusion limit for the dynamics of a large purely age structured population with closely matched birth and death rates. To this end we work out the technical details necessary to apply the general results in Méléard and Tran [19] to this particular case. This way we derive, starting from a logistic age-structured birth and death process, a Feller diffusion with drift and diffusion coefficients that are averages over the age distribution.

## 1 Feller diffusion limit with averages on the age distribution

We assume the population's initial size to be proportional to a parameter  $K$ , to be interpreted as the area to which the population is confined, that we will let grow to infinity while keeping the density constant by counting individuals with weight  $1/K$ . The population is assumed to be well mixed and its density is assumed to be limited by a fixed availability per unit of area of resources. Each individual is characterized by its physical age and the population at time  $t$  is described by the following point measure on  $\mathbb{R}_+$

$$(1) \quad X_t^K = \frac{1}{K} \sum_{i=1}^{N_t^K} \delta_{A_i(t)}(da),$$

where  $A_i(t)$  denotes the age of the  $i^{\text{th}}$  oldest individual at time  $t$  and  $N_t^K$  is the number of individuals alive at time  $t$ . The space of finite measures  $\mathcal{M}_F(\mathbb{R}_+)$  is equipped with the topology of weak convergence. Our processes live in the space of càdlàg paths  $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_F(\mathbb{R}_+))$  equipped with the Skorokhod topology. We scale time so that the life length and gestation length overall are inversely proportional to  $K$ . To achieve this, we choose the per capita birth and death rates to be of the form:

$$b^K(a) = K r(a) + \beta(a), \quad d^K(a, X_t^K) = K r(a) + \eta \langle X_t^K, 1 \rangle$$

where we denote by  $\langle \mu, f \rangle = \int f d\mu$  the integral of a function  $f$  with respect to the measure  $\mu$ . The order  $K$  terms in the birth and death rates are the same, to maintain the demographic balance. We assume that the function  $r(a)$  is positive, continuous, bounded and such that

$$(2) \quad \int_0^{+\infty} r(a) da = +\infty.$$

In this model, the individuals compete for resources, which is described by the logistic death term  $\eta \langle X_t^K, 1 \rangle$  where  $\eta \geq 0$ . The term  $\beta(a)$ , which is assumed positive, continuous and bounded, can be viewed as the growth rate of the population in absence of interaction. Finally, by choice of the time scale, the scale for age-structure corresponds to an aging velocity equal to  $K$ , so that the physical age of an individual born at time  $c$  is here  $a = K \times (t - c)$ . We shall refer to this combined scaling as ‘allometric’ after the alternative interpretation of the individual level relations as an inverse relation between birth rate, and mean lifetime and weight.

The chosen scaling of the population process leads to a diffusion limit. For populations with age structure, such limits have already been studied by various authors, but always for cases without interaction and with techniques based on Laplace characterizations that can no longer be used in the presence of a competition term (see *e.g.* [1, 2, 5, 7, 9, 16, 23]). Our results generalize [1, 2], where averaging results are proved for the case where birth and death rates do not depend on age: in the limit, these authors show that the age structure stabilizes to an exponential distribution. For cases with both age and interactions, the literature has mainly focused on the case without our allometric demography, proving convergence to a partial differential equation (PDE) (see *e.g.* [14, 21, 22]). In particular, if the birth and death rates are both equal to  $r(a)$  we recover the classical McKendrick-von Foerster PDE of demography [18, 10]:

$$(3) \quad \partial_t m(a, t) + \partial_a m(a, t) = -r(a)m(a, t), \quad m(0, t) = \int_0^{+\infty} r(a)m(a, t) da.$$

Let  $(\Omega, \mathcal{A}, \mathbb{P})$  be a probability space on which is defined a Poisson point measure  $Q(ds, di, d\theta)$  with intensity measure  $q(ds, di, d\theta) = ds n(di) d\theta$ , where  $ds$  and  $d\theta$  are Lebesgue measures on  $\mathbb{R}_+$  and where  $n(di)$  is the counting measure on  $\mathbb{N}$ . Following [22], we can use the measure  $Q(ds, di, d\theta)$  to define a stochastic differential equation (SDE) describing the evolution of the process  $\langle X_t^K, f \rangle$  for a bounded and boundedly differentiable test function  $f(a) \in \mathcal{C}_b^1(\mathbb{R}_+, \mathbb{R})$ :

$$(4) \quad \langle X_t^K, f \rangle = \langle X_0^K, f \rangle + \int_0^t K \langle X_s^K, f' \rangle ds + \frac{1}{K} \int_{[0, t] \times \mathbb{N} \times \mathbb{R}_+} \mathbf{1}_{i \leq K \langle X_{s-}^K, 1 \rangle} \{ \mathbf{1}_{\theta \leq Kr(A_i(s-)) + \beta(A_i(s-))} f(0) \\ - \mathbf{1}_{Kr(A_i(s-)) + \beta(A_i(s-)) < \theta \leq 2Kr(A_i(s-)) + \beta(A_i(s-)) + \eta \langle X_{s-}^K, 1 \rangle} f(A_i(s-)) \} Q(ds, di, d\theta).$$

In the sequel, we denote by  $(\mathcal{F}_t)_{t \in \mathbb{R}_+}$  the canonical filtration associated with  $Q$  and the initial conditions  $(X_0^K)_{K \geq 1}$ . When  $K$  tends to infinity, the aging velocity tends to infinity and simplification of the allometric birth and death rates  $Kr(a)$  is not direct since births are nonlocal (age is reset to 0). The idea is based on the observation that all terms of order  $K$  can be simplified when we compute the size of the population. However, since the rates depend on age, we have to account for the limiting age distribution.

**Theorem 1.1.** *Assume that the following limit in probability holds:*

$$(5) \quad \lim_{K \rightarrow +\infty} X_0^K(da) = m_0(a)da, \quad \text{with} \quad \sup_{K \in \mathbb{N}^*} \mathbb{E}(\langle X_0^K, 1 \rangle^3) < +\infty.$$

*Then:*

(i) *the sequence of processes  $(\langle X_t^K, 1 \rangle)_{K \geq 1}$  converges in distribution to the Feller diffusion:*

$$(6) \quad \bar{X}_t = \int_{\mathbb{R}_+} m_0(a) da + \int_0^t (\hat{\beta} \bar{X}_s - \eta \bar{X}_s^2) ds + \int_0^t \sqrt{2\hat{r} \bar{X}_s} dB_s$$

where  $B$  is a standard real Brownian motion,  $\widehat{\beta} = \int_{\mathbb{R}_+} \beta(a)\widehat{m}(a)da$  and  $\widehat{r} = \int_{\mathbb{R}_+} r(a)\widehat{m}(a)da$  with:

$$(7) \quad \widehat{m}(a) = \frac{\exp(-\int_0^a r(\alpha)d\alpha)}{\int_0^{+\infty} \exp(-\int_0^a r(\alpha)d\alpha)da}.$$

(ii) for every  $t > 0$ , the sequence of measures  $(X_t^K(da))_{K \geq 1}$  converges in distribution to  $\bar{X}_t \widehat{m}(a)da$ .

The proof of Theorem 1.1 is detailed in the next section. The theorem states that the age distribution, as the fast component, stabilizes to a non-trivial equilibrium  $\widehat{m}(a)$  of the PDE (3), with only the order  $K$  in (4) as birth and death rates. The slow component, the size of the population, is then described by a Feller diffusion in which coefficients are averaged over  $\widehat{m}(a)$ . The latter limit is similar to the limit that was already derived for the case without age-structure by [3].

One use of the result is for the approximate calculation of extinction probabilities:

**Proposition 1.2.** *For the diffusion (6):*

(i) when  $\eta > 0$ , we have almost sure extinction in finite time.

(ii) when  $\eta = 0$ ,  $\mathbb{P}(\exists t \in \mathbb{R}_+, \bar{X}_t = 0) = \exp(-\widehat{\beta} \int_0^{+\infty} m_0(a)da/\widehat{r})$ .

*Proof.* Notice that 0 is an absorbing point. When  $\eta > 0$ , we can prove almost sure extinction by exhibiting a Lyapounov function (see [13, p.235] or [19]). For  $\eta = 0$ , we can then adapt the computation of [13, p.236] and obtain that:

$$\mathbb{P}(\bar{X}_t = 0) = \exp\left(-\frac{e^{\widehat{\beta}t} \int_0^{+\infty} m_0(a)da}{\widehat{r}(e^{\widehat{\beta}t} - 1)/\widehat{\beta}}\right).$$

Letting  $t \rightarrow +\infty$ , we obtain the announced result. ■

## 2 Proof of Theorem 1.1

The proof is divided into several steps. From (4) we see that for a test function  $f \in C_b^1(\mathbb{R}_+, \mathbb{R})$  the process:

$$(8) \quad M_t^{f,K} = \langle X_t^K, f \rangle - \langle X_0^K, f \rangle - \int_0^t \langle X_s, Kf'(\cdot) + (Kr(\cdot) + \beta(\cdot))f(0) - (Kr(\cdot) + \eta\langle X_s^K, 1 \rangle)f(\cdot) \rangle ds,$$

which can be written as an integral with respect to the compensated Poisson point measure of  $Q(ds, di, d\theta)$ , is a local martingale started at 0. If we introduce  $\tau_n = \inf\{t \geq 0, \langle X_t^K, 1 \rangle \geq n\}$ , then the process  $M_{\tau_n \wedge \cdot}^{f,K}$  is a square integrable martingale with predictable quadratic variation:

$$\langle M^{f,K} \rangle_{t \wedge \tau_n} = \int_0^{\tau_n \wedge t} \left( \langle X_s^K, r(\cdot)f^2(0) + r(\cdot)f^2(\cdot) + \frac{\beta(\cdot)f^2(0) + \eta\langle X_s^K, 1 \rangle f^2(\cdot)}{K} \rangle \right) ds.$$

As noticed before, the aging speed tends to infinity and it is difficult to keep track of the individual. Moreover, births are non-local since the age of a new individual is always reset to 0, inducing an asymmetry between an individual and its parent. If we consider the test function  $f \equiv 1$ , the derivative with respect to age disappears and the allometric birth and death terms compensate each other. Thus:

$$(9) \quad M_t^{1,K} = \langle X_t^K, 1 \rangle - \langle X_0^K, 1 \rangle - \int_0^t \left( \langle X_s^K, \beta \rangle - \eta \langle X_s^K, 1 \rangle^2 \right) ds$$

defines a local martingale started at 0. The stopped process  $M_{\tau_n \wedge \cdot}^{1,K}$  has predictable quadratic variation:

$$\langle M^{1,K} \rangle_{t \wedge \tau_n} = \int_0^{t \wedge \tau_n} \left( 2\langle X_s^K, r \rangle + \frac{\langle X_s^K, \beta \rangle + \eta \langle X_s^K, 1 \rangle^2}{K} \right) ds.$$

As seen below, checking the tightness of the total mass processes  $(\langle X_t^K, 1 \rangle)_{K \geq 1}$  is classical as soon as moment estimates are proved. However, for the identification of the martingale problem satisfied by the limiting values, we still need to tackle the age distribution as the rate  $\beta(a)$  depends on age.

**1: Moment estimates.** Under Assumptions (5), we will show by following [3] that

$$(10) \quad \sup_{K \in \mathbb{N}^*} \sup_{t \leq T} \mathbb{E}(\langle X_t^K, 1 \rangle^3) < +\infty \quad \text{and} \quad \sup_{K \in \mathbb{N}^*} \mathbb{E}(\sup_{t \leq T} \langle X_t^K, 1 \rangle^2) < +\infty.$$

Indeed:

$$\begin{aligned} \langle X_t^K, 1 \rangle^3 &\leq \langle X_0^K, 1 \rangle^3 \\ &+ \int_0^t \int_{\mathbb{N} \times \mathbb{R}_+} \mathbf{1}_{i \leq K} \langle X_{s-}^K, 1 \rangle \left[ \mathbf{1}_{\theta \leq Kr(A_i(s-)) + \beta(A_i(s-))} \left( (\langle X_{s-}^K, 1 \rangle + \frac{1}{K})^3 - \langle X_{s-}^K, 1 \rangle^3 \right) \right. \\ &\left. + \mathbf{1}_{Kr(A_i(s-)) + \beta(A_i(s-)) < \theta \leq 2Kr(A_i(s-)) + \beta(A_i(s-)) + \eta \langle X_{s-}^K, 1 \rangle} \left( (\langle X_{s-}^K, 1 \rangle - \frac{1}{K})^3 - \langle X_{s-}^K, 1 \rangle^3 \right) \right] dQ. \end{aligned}$$

Using that  $x^3 - y^3 = (x - y)(x^2 + xy + y^2)$ , taking the expectation and using Gronwall's lemma:

$$\begin{aligned} \mathbb{E}(\langle X_{t \wedge \tau_n}^K, 1 \rangle^3) &= \mathbb{E}(\langle X_0^K, 1 \rangle^3) \\ &+ \mathbb{E} \left( \int_0^{t \wedge \tau_n} ds \int_{\mathbb{R}_+} X_s^K(da) \left[ 6r(a) \langle X_s^K, 1 \rangle + \beta(a) (3 \langle X_s^K, 1 \rangle^2 + \frac{3 \langle X_s^K, 1 \rangle}{K} + \frac{1}{K^2}) \right. \right. \\ &\quad \left. \left. - \eta \langle X_s^K, 1 \rangle (3 \langle X_s^K, 1 \rangle^2 - \frac{3 \langle X_s^K, 1 \rangle}{K} + \frac{1}{K^2}) \right] \right) \\ &\leq \mathbb{E}(\langle X_0^K, 1 \rangle^3) + \int_0^t C \mathbb{E}(1 + \langle X_{s \wedge \tau_n}^K, 1 \rangle^3) ds \leq \left( \mathbb{E}(\langle X_0^K, 1 \rangle^3) + CT \right) e^{CT} \end{aligned}$$

which is finite thanks to (5) and where  $C$  is a constant that does not depend on  $K$  nor on  $n$ . The upper bound being independent of  $n$ , we necessarily have that  $\lim_{n \rightarrow +\infty} \tau_n = +\infty$  a.s. By using Fatou's lemma we can get rid of the stopping time  $\tau_n$  in the l.h.s. This proves the first part of (10). For the second part, using (9) and Cauchy-Schwarz' inequality:

$$\sup_{u \leq t} \langle X_{u \wedge \tau_n}^K, 1 \rangle^2 \leq 3 \langle X_0^K, 1 \rangle^2 + 3 \sup_{u \leq t} |M_{u \wedge \tau_n}^{1,K}|^2 + 3T \int_0^t \|\beta\|_\infty \sup_{u \leq s} \langle X_s^K, 1 \rangle^2 ds.$$

Taking the expectation and using Doob's inequality, Gronwall's lemma and the first estimate of (10) completes the proof of (10). As a consequence, we can show that the martingales (8) and (9) are square integrable martingales.

**2: Tightness of the mass process.** Thanks to (10), the family of marginal laws  $(\langle X_t^K, 1 \rangle)_{K \geq 1, t \in [0, T]}$  form a tight family of real random variables. Then, Aldous-Rebolledo criterion (see *e.g.* [15]) can be checked for the predictable finite variation part of the semi-martingale  $\langle X_t^K, 1 \rangle$  and for  $\langle M^{1,K} \rangle$ . Let  $(S_K, T_K)_K$  be a sequence of stopping times such that for every  $K$ ,  $S_K \leq T_K \leq T \wedge (S_K + \delta)$ . Since

$$\mathbb{P} \left( \left| \int_{S_K}^{T_K} (\langle X_s^K, \beta \rangle - \eta \langle X_s^K, 1 \rangle^2) ds \right| > \varepsilon \right) \leq \frac{\delta}{\varepsilon} \left( \|\beta\|_\infty \mathbb{E}(\sup_{t \leq T} \langle X_t^K, 1 \rangle) + \eta \mathbb{E}(\sup_{t \leq T} \langle X_t^K, 1 \rangle^2) \right),$$

which can be made smaller than  $\varepsilon$  by (10) and for  $\delta$  small enough. A similar estimate is derived for  $\langle M^{1,K} \rangle$ . Thus, the sequence  $(\langle X_t^K, 1 \rangle)_{K \geq 1}$  is tight in  $\mathbb{D}([0, T], \mathbb{R}_+)$ .

**3: Tightness of the family of marginal laws  $(X_t^K)_{K \geq 1, t \in [0, T]}$  in  $\mathcal{M}_F(\mathbb{R}_+)$ .** Modifying the indicators in (4), it is possible to couple for each  $K$  the process  $X^K$  with a process  $Y^K$  without

competition where individuals give birth at rate  $Kr(a) + \beta(a)$  and die with rate  $Kr(a)$ . All the individuals in  $X^K$  are present in  $Y^K$  with independent and longer lifelengths. The lifelength of the  $i^{\text{th}}$  individual living at time  $t$  is hence smaller than a random variable  $D_i^K(t)$  whose distribution is characterized by its survival function  $S^K(\ell) = \exp(-\int_0^\ell Kr(Ku)du)$ . Since the aging velocity is  $K$  the probability that an individual lives until age  $\alpha$  is  $S^K(\alpha/K) = \exp(-\int_0^\alpha r(a)da)$ . Then for positive  $\alpha$ ,  $\varepsilon$  and  $n > 0$ :

$$\begin{aligned} \mathbb{P}(X_t^K([0, \alpha]^c) > \varepsilon) &\leq \mathbb{P}\left(\sum_{i=1}^{N_t^K} \mathbf{1}_{A_i(t) \geq \alpha} > K\varepsilon, N_t^K \leq nK\right) + \mathbb{P}(N_t^K > nK) \\ &\leq \mathbb{P}\left(\sum_{i=1}^{nK} \mathbf{1}_{D_i(t) \geq \alpha/K} > K\varepsilon\right) + \frac{\mathbb{E}(\langle X_t^K, 1 \rangle)}{n}. \end{aligned}$$

The second term is upper bounded by  $\varepsilon/2$  for sufficiently large  $n$  thanks to (10). As for the first term, using Bernstein inequality (see *e.g.* [12, p.241]):

$$\begin{aligned} \mathbb{P}\left(\sum_{i=1}^{nK} \mathbf{1}_{D_i(t) \geq \alpha/K} > K\varepsilon\right) &= \mathbb{P}\left(\sum_{i=1}^{nK} \left\{\mathbf{1}_{D_i(t) \geq \alpha/K} - S^K\left(\frac{\alpha}{K}\right)\right\} > K\left\{\varepsilon - nS^K\left(\frac{\alpha}{K}\right)\right\}\right) \\ &\leq \exp\left(-\frac{K^2(\varepsilon - nS^K(\alpha/K))^2}{2(4nK + \frac{2K(\varepsilon - nS^K(\alpha/K))}{3})}\right) \end{aligned}$$

Choosing  $\alpha = \alpha(n)$  sufficiently large implies that  $(\varepsilon - nS^K(\alpha/K)) > \varepsilon/2$ . Then, it is possible to choose  $K_0 = K_0(\alpha, n)$  sufficiently large, so that the r.h.s. is upper bounded by  $\varepsilon/2$  for all  $K \geq K_0$ . Note also that since the upper bound does not depend on  $t \in [0, T]$  the choices of  $\alpha$  and  $K_0$  are independent of  $t \in [0, T]$ . This provides the expected tightness.

**4: Tightness of the family of measures**  $(\Gamma^K(dt, da) = X_t^K(da)dt)_{K \geq 1}$ . We follow the approach of Kurtz [17]. Since we have to deal with the fast component in  $\mathbb{D}([0, T], \mathcal{M}_F(\mathbb{R}_+))$ , we forget that we deal with processes and rather consider the measures  $(\Gamma^K)_{K \geq 1}$  in  $\mathcal{M}_F([0, T] \times \mathbb{R}_+)$ . We have for  $\alpha > 0$ :

$$\begin{aligned} \Gamma^K\left(\left([0, T] \times \mathbb{R}_+\right) \setminus \left([0, T] \times [0, \alpha]\right)\right) &= \mathbb{E}\left(\int_0^T X_t^K([0, \alpha]^c)dt\right) \\ &\leq \int_0^T \left(\varepsilon \mathbb{P}(X_t^K([0, \alpha]^c) \leq \varepsilon) + \mathbb{E}(\langle X_t^K, 1 \rangle \mathbf{1}_{X_t^K([0, \alpha]^c) > \varepsilon})\right)dt \\ &\leq T\varepsilon + \int_0^T \mathbb{E}(\langle X_t^K, 1 \rangle^2)^{1/2} \mathbb{P}(X_t^K([0, \alpha]^c) > \varepsilon)^{1/2} dt \leq T\varepsilon + C(T)\sqrt{\varepsilon}. \end{aligned}$$

This proves the tightness of  $(\Gamma^K)_{K \geq 1}$  in  $\mathcal{M}_F([0, T] \times \mathbb{R}_+)$ .

**5: Identification of the limiting values of  $(\Gamma^K)_{K \geq 1}$ .** The sequence  $(\Gamma^K, \langle X^K, 1 \rangle)_{K \in \mathbb{N}^*}$  is tight in  $\mathcal{M}_F([0, T] \times \mathbb{R}_+) \times \mathbb{D}([0, T], \mathbb{R}_+)$  as each of its components are. By Prohorov's theorem (see *e.g.* [8]) we can extract a subsequence that converges in distribution to a limiting value  $(\Gamma, \bar{X})$  which belongs to  $\mathcal{M}_F([0, T] \times \mathbb{R}_+) \times \mathcal{C}([0, T], \mathbb{R})$ . Our purpose is now to characterize the latter.

Let  $\varphi(s)$  be a continuous bounded function. From the definition of  $\Gamma^K$  we have for every  $t \in [0, T]$ :

$$\int_0^t \int_{\mathbb{R}_+} \varphi(s) \Gamma^K(da, ds) = \int_0^t \varphi(s) \langle X_s^K, 1 \rangle ds.$$

By letting  $K$  tend to infinity, we obtain that the marginal measure of  $\Gamma(da, ds)$  is  $\bar{X}_s ds$  and there exists a transition probability  $\gamma_s(da)$  such that  $\Gamma(da, ds) = \gamma_s(da) \bar{X}_s ds$ . Recall that for a test function

$f \in \mathcal{C}_b^1(\mathbb{R}_+, \mathbb{R})$  we have (8). Let us write:

$$\begin{aligned}\frac{M_t^{f,K}}{K} &= A_t^K + B_t^K \\ A_t^K &= \frac{\langle X_t^K, f \rangle - \langle X_0^K, f \rangle}{K} + \int_0^t \int_{\mathbb{R}_+} \left( \frac{\beta(a)}{K} f(0) - \frac{\eta \langle X_s^K, 1 \rangle}{K} f(a) \right) X_s^K(da) ds \\ B_t^K &= \int_0^t \int_{\mathbb{R}_+} (f'(a) + r(a)(f(0) - f(a))) X_s^K(da) ds.\end{aligned}$$

From (10),  $\mathbb{E}(\sup_{t \leq T} A_t^K) \rightarrow 0$  when  $K \rightarrow +\infty$ . Since  $\Xi \mapsto \int_0^t \int_{\mathbb{R}_+} (f'(a) + r(a)(f(0) - f(a))) \Xi(da, ds)$  is continuous at  $\Gamma$ , the last term converges in distribution for every  $t \in [0, T]$  towards

$$(11) \quad \bar{M}_t^f = \int_0^t \int_{\mathbb{R}_+} (f'(a) + r(a)(f(0) - f(a))) \bar{X}_s \gamma_s(da) ds.$$

Let  $H_s \in \mathcal{F}_s$ . Since  $M^{f,K}$  is a square integrable martingale, we have uniform integrability of the families  $(M_t^{f,K}/K)_{K \geq 1}$  for every  $t \in [0, T]$ . Hence:

$$\mathbb{E}(\bar{M}_t^f H_s) = \mathbb{E}\left(\lim_{K \rightarrow +\infty} \frac{M_t^{f,K}}{K} H_s\right) = \lim_{K \rightarrow +\infty} \mathbb{E}\left(\frac{M_t^{f,K}}{K} H_s\right) = \lim_{K \rightarrow +\infty} \mathbb{E}\left(\frac{M_s^{f,K}}{K} H_s\right) = \mathbb{E}\left(\bar{M}_s^f H_s\right).$$

This shows that  $\bar{M}^f$  is a martingale, but since (11) gives that it is also continuous with finite variation, it is indistinguishable from the null process. Hence almost-surely and  $dt$ -almost everywhere:

$$(12) \quad \int_{\mathbb{R}_+} (f'(a) + r(a)(f(0) - f(a))) \bar{X}_t \gamma_t(da) = 0.$$

Choosing in (12) a test function of the form  $f(a) = \varphi(0) + \int_0^a \varphi(\alpha) d\alpha$ , with continuous and bounded  $\varphi$ , gives that:

$$\bar{X}_t \langle \gamma_t, \varphi \rangle = \bar{X}_t \int_{\mathbb{R}_+} \varphi(\alpha) \left( \int_{\alpha}^{+\infty} r(a) \gamma_t(da) \right) d\alpha.$$

If  $\bar{X}_t = 0$ , then  $\Gamma(da, ds) = 0$ . On  $\{\bar{X}_t > 0\}$ , the above equality tells us that  $\gamma_t(da)$  is absolutely continuous with respect to the Lebesgue measure with a density  $\hat{m}_t(a)$  that satisfies for all  $a \in \mathbb{R}_+$ ,  $\hat{m}_t(a) = \int_a^{+\infty} r(\alpha) \hat{m}_t(\alpha) d\alpha$ . It results that  $a \mapsto \hat{m}_t(a)$  is infinitely differentiable and solves  $\partial_a \hat{m}_t(a) = -r(a) \hat{m}_t(a)$  which characterizes the stationary solution of the McKendrick-von Foerster equation (3). The solution of this equation is of the form  $\hat{m}_t(a) = \hat{m}_t(0) \exp(-\int_0^a r(\alpha) d\alpha)$ , and since  $\gamma_t(da)$  is a probability measure:

$$1 = \int_0^{+\infty} \hat{m}_t(a) da = \hat{m}_t(0) \int_0^{+\infty} e^{-\int_0^a r(\alpha) d\alpha} da \quad \Leftrightarrow \quad \hat{m}_t(0) = \frac{1}{\int_0^{+\infty} \exp(-\int_0^a r(\alpha) d\alpha) da}.$$

This provides (7) and all the limiting values of  $(\Gamma^K)_{K \geq 1}$  are of the form  $\bar{X}_t \hat{m}(a) da$  where  $\bar{X}$  is a limiting distribution of  $(X^K)_{K \geq 1}$ . Our purpose is now to identify  $\bar{X}$  as the unique strong solution of the diffusion (9) so that the sequence  $(\Gamma^K)_{K \geq 1}$  converges in distribution to its unique limiting value.

**6: Identification of  $\bar{X}$ .** Let us consider for  $n \in \mathbb{N}^*$ , the times  $t_1 < \dots < t_n < s < t$  and the continuous bounded functions  $\psi_1, \dots, \psi_n$ . We introduce the following map:

$$\Psi_{s,t}(Y) = \left[ Y_t - Y_s - \int_s^t (\hat{\beta} Y_s - \eta Y_s^2) ds \right] \psi_1(Y_{t_1}) \dots \psi_n(Y_{t_n}).$$

Since the limiting values of  $(\langle X^K, 1 \rangle)_{K \geq 1}$  are necessarily continuous,  $\Psi$  is continuous at  $\bar{X}$ . We have:

$$\begin{aligned} \Psi_{s,t}(\langle X^K, 1 \rangle) &= \psi_1(\langle X_{t_1}^K, 1 \rangle) \dots \psi_n(\langle X_{t_n}^K, 1 \rangle) \left[ A_{s,t}^K + B_{s,t}^K \right] \\ A_{s,t}^K &= \int_s^t (\langle X_s^K, \beta \rangle - \widehat{\beta} \bar{X}_s) ds, \quad B_{s,t}^K = \int_s^t \eta (\langle X_s^K, 1 \rangle^2 - \bar{X}_s^2) ds. \end{aligned}$$

As  $\beta(a)$  is continuous and as  $\Gamma^K$  converges to  $\widehat{m}(a) da \bar{X}_s ds$ ,  $A_{s,t}^K$  converges to zero. Thanks to (10),  $\mathbb{E}(|A_{s,t}^K|) \rightarrow 0$  when  $K \rightarrow +\infty$ . A similar result holds for  $E(|B_{s,t}^K|)$  since  $\bar{X}$  is a limiting value of  $\langle X^K, 1 \rangle$ . We deduce that for every  $s$  and  $t$ ,  $\mathbb{E}(|\Psi_{s,t}(\langle X^K, 1 \rangle)|) \rightarrow 0$  and for all  $t$ ,  $M_t = \bar{X}_t - \int_{\mathbb{R}_+} m_0(a) da - \int_0^t (\widehat{\beta} \bar{X}_s - \eta \bar{X}_s^2) ds$  is a martingale. To compute its bracket, we first apply Itô's formula to  $M$ , yielding that

$$(13) \quad \bar{X}_t^2 - \left( \int_{\mathbb{R}_+} m_0(a) da \right)^2 - \int_0^t 2\bar{X}_s (\widehat{\beta} \bar{X}_s - \eta \bar{X}_s^2) ds - \langle M \rangle_t$$

is a martingale. Moreover, using Itô's formula with (4), the following process is also a martingale:

$$\begin{aligned} \langle X_t^K, 1 \rangle^2 - \langle X_0^K, 1 \rangle^2 - \int_0^t \int_{\mathbb{R}_+} \left( (Kr(a) + \beta(a))(2\langle X_s^K, 1 \rangle + \frac{1}{K}) \right. \\ \left. - (Kr(a) + \eta \langle X_s^K, 1 \rangle)(2\langle X_s^K, 1 \rangle - \frac{1}{K}) \right) X_s^K(da) ds. \end{aligned}$$

which, by arguments similar to the ones above, implies that

$$(14) \quad \bar{X}_t^2 - \bar{X}_0^2 - \int_0^t \left[ 2\bar{X}_s (\widehat{\beta} \bar{X}_s - \eta \bar{X}_s^2) + 2\widehat{r} \bar{X} \right] ds$$

is a martingale. By identification of (13) and (14),  $\langle M \rangle_t = 2\widehat{r} \int_0^t \bar{X}_s ds$ , and it is classical to show that on an enlarged filtration space, there exists a Brownian motion  $(B_t)_{t \in [0, T]}$  such that  $M_t = \int_0^t \sqrt{2\widehat{r} \bar{X}_s} dB_s$ . Hence  $\bar{X}$  solves the Feller equation (6), for which strong uniqueness holds.  $\square$

**Acknowledgements:** This work benefited from the support of the ANR MANEGE (ANR-09-BLAN-0215), from the ‘‘Chair Modélisation Mathématique et Biodiversité of Veolia Environnement-Ecole Polytechnique-Museum National d’Histoire Naturelle-Fondation X’’. It also benefited from the visit of both authors to the Institute for Mathematical Sciences of the National University of Singapore in 2011.

## References

- [1] K. Athreya, S. Athreya, and S. Iyer. Super-critical age dependent branching Markov processes and their scaling limits. *Bernoulli*, 17(1):138–154, 2011.
- [2] A. Bose and I. Kaj. Diffusion approximation for an age-structured population. *Annals of Applied Probabilities*, 5(1):140–157, 1995.
- [3] N. Champagnat, R. Ferrière, and S. Méléard. From individual stochastic processes to macroscopic models in adaptive dynamics. *Stochastic Models*, 24:2–44, 2008.
- [4] B. Charlesworth. *Evolution in Age structured Population*. Cambridge University Press, 2 edition, 1994.
- [5] D.A. Dawson, L.G. Gorostiza, and Z. Li. Nonlocal branching superprocesses and some related models. *Acta Applicandae Mathematicae*, 74:93–112, 2002.
- [6] M. Durinx, J.A.J. Metz, and G. Meszéna. Adaptive dynamics for physiologically structured models. *Journal of Mathematical Biology*, 5(56):673–742, 2008.



- [7] E.B. Dynkin. Branching particle systems and superprocesses. *Annals of Probability*, 19:1157–1194, 1991.
- [8] S.N. Ethier and T.G. Kurtz. *Markov Processus, Characterization and Convergence*. John Wiley & Sons, New York, 1986.
- [9] K. Fleischmann, V.A. Vatutin, and A. Wakolbinger. Branching systems with long-living particles at the critical dimension. *Theoretical Probability and its Applications*, 47(3):429–454, 2002.
- [10] H. Von Foerster. Some remarks on changing populations. In Grune & Stratton, editor, *The Kinetics of Cellular Proliferation*, pages 382–407, New York 1959.
- [11] N. Fournier and S. Méléard. A microscopic probabilistic description of a locally regulated population and macroscopic approximations. *Ann. Appl. Probab.*, 14(4):1880–1919, 2004.
- [12] W. Härdle, G. Kerkycharian, D. Picard, and A. Tsybakov. *Wavelets, Approximation, and Statistical Applications*, volume 129 of *Lecture Notes in Statistics*. Springer, New York, 1987.
- [13] N. Ikeda and S. Watanabe. *Stochastic Differential Equations and Diffusion Processes*, volume 24. North-Holland Publishing Company, 1989. Second Edition.
- [14] P. Jagers and F. Klebaner. Population-size-dependent and age-dependent branching processes. *Stochastic Processes and their Applications*, 87:235–254, 2000.
- [15] A. Joffe and M. Métivier. Weak convergence of sequences of semimartingales with applications to multitype branching processes. *Advances in Applied Probability*, 18:20–65, 1986.
- [16] I. Kaj and S. Sagitov. Limit processes for age-dependent branching particle systems. *Journal of Theoretical Probability*, 11(1):225–257, 1998.
- [17] T.G. Kurtz. Averaging for martingale problems and stochastic approximation. In Springer, editor, *Applied stochastic analysis (New Brunswick, NJ, 1991)*, volume 177 of *Lectures Notes in Control and Inform. Sci.*, pages 186–209, Berlin, 1992.
- [18] A.G. McKendrick. Applications of mathematics to medical problems. *Proc. Edin. Math.Soc.*, 54:98–130, 1926.
- [19] S. Méléard and V.C. Tran. Slow and fast scales for superprocess limits of age-structured populations. submitted: <http://fr.arxiv.org/abs/1006.5136>.
- [20] J.A.J. Metz. Thoughts on the geometry of meso-evolution: collecting mathematical elements for a post-modern synthesis. In F.A.C.C. Chalub and J.F. Rodrigues, editors, *The Mathematics of Darwins Legacy*, Basel, 2011. Birkhauser.
- [21] K. Oelschläger. Limit theorem for age-structured populations. *The Annals of Probability*, 18(1):290–318, 1990.
- [22] V.C. Tran. Large population limit and time behaviour of a stochastic particle model describing an age-structured population. *ESAIM: P&S*, 12:345–386, 2008.
- [23] F.J.S. Wang. A central limit theorem for age- and density-dependent population processes. *Stochastic Processes and their Applications*, 5:173–193, 1977.